BOREAL ENVIRONMENT RESEARCH 17: 291–304
ISSN 1239-6095 (print) ISSN 1797-2469 (online) Helsinki 29 June 2012

Rearing environment affects important life skills in pikeperch (*Sander lucioperca*)

Ida Ahlbeck* and Per B. Holliland

*Department of Systems Ecology, Stockholm University, SE-106 91 Stockholm, Sweden (*corresponding author's e-mail: ida@ecology.su.se)*

Received 28 Feb. 2011, final version received 31 Oct. 2011, accepted 8 Sep. 2011

Ahlbeck, I. & Holliland, P. B. 2012: Rearing environment affects important life skills in pikeperch (*Sander lucioperca*). *Boreal Env. Res.* 17: 291–304.

The effect of rearing environment on the behaviour of young-of-the-year pikeperch (*Sander lucioperca*) bred at three different production facilities was investigated. Two groups were reared in semi-natural ponds and one group in indoor tanks. Exploratory, foraging and anti-predator behaviours were studied in aquarium experiments. There were no significant differences between pond- and tank-reared fish in reluctance to explore their new environment, but pond-reared fish spent significantly more time in macro-vegetation. Pond-reared fish were significantly faster to start foraging on live prey (*Neomysis integer*) that they had not encountered before. As compared with tank-reared fish, pond-reared fish were also significantly more active in their anti-predator response. Rearing environment obviously influences the development of important life skills. These differences may impact the success rate when stocking young-of-the-year pikeperch into natural waters.

Introduction

Fish are reared for two main purposes: human consumption, or stocking to introduce or strengthen already present populations in natural waters. Stocking is, however, a controversial practice with respect to both genetic and behavioural (Kreuger and May 1991, Einum and Fleming 1997, Dannewitz *et al*. 2010) effects on the wild population. There are also concerns about behavioural deficiencies in the stocked fish, as fish from artificial rearing environments often lack ontogenetic experiences required for proper behavioural development (Kelly *et al*. 2005). For successful stocking, rearing conditions should make fish as fit as possible to minimize mortality rates upon release into the wild. Among others, stocked fish should be able to develop appropriate behaviour patterns already prior to stocking (Brännäs and Johnsson 2008).

Physical and social environment strongly affects the ability of fish to acquire important life skills (Magnhagen *et al*. 2008) such as exploratory behaviour, ability to feed on natural prey, and ability to avoid predators. To improve important aspects of their behaviour, reared fish can be trained before release. For example, naïve salmon become more efficient feeders on live prey after observing experienced fish (Brown *et al*. 2003a), and hatchery-reared fish can be conditioned to avoid predators by repeated exposures to the odours of conspecific-fed predator (Vilhunen 2006). Fish can even learn from hetero-specifics (Coolen *et al*. 2003). Results from training are, however, equivocal and several studies were unable to show improved behaviour

Editor in charge of this article: Outi Heikinheimo

after training (e.g. Berejikian 1996, Maynard *et al*. 1996a) probably due to too short exposure times. Training by observing more experienced individuals may also fail due to lower social learning from tutors shown in fish reared in plain environments (Strand *et al*. 2010). Instead of counteracting behavioural deficiencies by training, the rearing environment can be designed to provide conditions that favour the development of adequate behaviours. Increased environmental complexity has been proved to promote behavioural and neuronal plasticity as well as learning in fish, increasing survival after stocking (e.g., Braithwaite and Salvanes 2005, Kishlinger and Newitt 2006, Spence *et al*. 2011). Braithwaite and Salvanes (2005) showed that young cod (*Gadus morhua*) exposed to variable spatial and foraging cues during rearing became more explorative and efficient in feeding on live prey.

Increasing the environmental complexity in the production facility may, however, come with the cost of a decreased growth rate of the fish. With the generally negative relationship between size and *in situ* mortality rate (e.g. McGurk 1986, Ellis and Gibson 1995, Juanes and Conover 1994) it can be favourable to have as large stocking fish as possible. This can be achieved by intensive farming with high quality food available *ad libitum*. In practice, the food is often artificial, since natural prey can be difficult to obtain in sufficient quantities.

In Sweden, pikeperch (*Sander lucioperca*) is commonly stocked as young-of-the-year (YOY) in late summer and autumn. Before stocking, these fish were most often reared in ponds on naturally occurring food, but in recent years production has also started in tanks in indoor facilities with artificial food. No results have been presented on how pikeperch is affected by differences in rearing conditions. In this study, we compare three different aspects of behaviour in YOY pikeperch that were produced in two different ponds and in one indoor-tank facility. The three behaviours studied (exploration of a new environment, feeding on a novel live prey and response to a predator) are such that we consider them to represent important life skills that are likely to affect fish survival shortly after stocking.

Material and methods

Pikeperch from three commercial breeders were used. All fish originated from wild adults that were caught just before spawning in Swedish Lake Hjälmaren. The pikeperch in Lake Hjälmaren is genetically homogenous all belonging to the same population (Dannewitz *et al*. 2010). Two of the breeders used outdoor semi-natural rearing ponds, which were in many aspects comparable to natural conditions with live prey, structural complexity, predators (e.g. birds and mink), and natural light and temperature regimes. Pond 1 had an area of approximately 160 000 m^2 and a maximum depth of ~2 m. Corresponding values for pond 2, were 90 000 m^2 and 5 m. The third breeder used indoor tanks (5 m^3) with a fixed feeding and light regime, lacking any structural complexity and natural variability. These fish were fed artificial food. Harvest dates were September 8 for Pond 1, September 13 for Tank, September 23 for Pond 2 and harvest temperatures (mean ± SD) were 14 ± 1 °C for the ponds and 23 °C for tank. The rearing densities were approximately 2500 times greater in the tank than in the ponds (estimate based on the data from Pond 2 and Tank). Cannibalistic individuals were present in the ponds but not in the tank. However, there were no data on the extent of cannibalism in the ponds.

Before the tests started, 100 randomly selected pikeperch from each breeder were held separately in three 500-l aquaria at 14 ± 1.5 °C (mean ± SD). The pond-bred fish had gravel and plastic plants in their tank whereas the tank-bred fish had a bare tank covered in black plastic sheets to mimic the environmental situation previously experienced. The pond-reared fish were fed freshwater zooplankton *ad libitum* and the tank-reared fish were fed pellet food *ad libitum*. All fish had a 12 hour day/night regime. Each group was left to settle in their new environment for seven days before tests were performed.

Although the fish were of the same age (four months old) a noticeable size difference existed among the different breeders. Tank-bred fish were significantly larger than the pond-bred fish (mean ± SE, Tank (n = 20): length = 110 ± 3 mm, weight = 13 ± 1 g; Pond 1 (n = 20): 76 ± 1 mm, 4 ± 0.3 g; Pond 2 (n = 20): 63 ± 2 mm, 3 ± 0.1 g;

ANOVA with Tukey's post hoc comparisons: all differences significant at $p < 0.00001$). The three groups also differed significantly in Fulton's condition index (mean ± SE, Tank ($n = 20$): 0.34 ± 0.02; Pond 1 ($n = 20$): 0.18 ± 0.01; Pond 2 ($n = 20$): 0.12 ± 0.004; ANOVA with Tukey's post hoc comparisons: all differences significant at $p < 0.00001$). In tank-bred fish, damage to eyes and worn fins were common. In the pond-bred fish, fungal infections were common, but infected fish were removed and destroyed. The tank-reared fish were also observed to have a different swimming behaviour as compared with that of the pond fish: they were mostly resting on the tank floor swimming only very shortly or swimming head down. They also reacted less to overhead movements than did pond-reared fish. These traits were only observed in the holding tanks and not quantitatively measured. No apparently damaged or sick fish were used in the tests. All groups were feeding well in the holding tanks.

Three behavioural tests were used to determine the effects of rearing environment on pikeperch. All tests were carried out during late September and early October 2010 in 50-l test aquaria (60 × 30 × 30 cm), observed from behind a black screen. In all trials, the water temperature (mean ± SD) was 14 ± 1.5 °C. All fish were randomly selected from the holding tank.

Exploratory behaviour

Three sides of the test aquarium were covered with black plastic sheets, leaving the long end facing the observers uncovered. The bottom of the aquarium was covered with gravel. The aquarium was divided into three "habitats". On the left-hand side of the test aquarium, plastic plants occupied one quarter of the volume of the tank; on the right-hand side of the aquarium a white, non-transparent plastic "start box" occupied one quarter of the tank bottom, and the area between the start box and the plastic plant was open. One fish was placed in the start box and allowed to acclimatize for 10 min. After this time, the observer used a thin line to slowly open the lid of the box from behind the screen. The time until the fish left the box was recorded. If the fish had not left the box after 30 minutes, the test was ended. If the fish had left the box, its position in the aquarium was recorded every 15 seconds for 10 min. Twenty trials for each breeder were run with a naïve fish in each trial.

Feeding on live prey

Three sides of the test aquarium were covered with black plastic sheets, leaving the long end facing the observers uncovered. The bottom of the tank was covered with gravel with a plastic plant in the left-hand-side corner. Five pikeperch were placed in an aquarium where mysids (*Neomysis integer*) were present at a density of 15 mysids per litre. Mysids were a previously unknown food source to all fish. The fish had been starved for 24 hours to increase feeding motivation. The time taken until the first attack on prey was recorded for each fish in the group. In this experiment, only fish from Pond 2 and tank-reared fish were used. Ten trials per rearing group were run with five naïve fish in each trial. The trial was ended when all fish attacked prey at least once, or after 60 minutes. The fish were observed by two observers that had two or three focal individuals to monitor during the trial to enable correct assessment of time to first caught prey.

Anti-predator response

Two test aquaria were placed next to each other separated by a removable cardboard divider to prevent visibility between the aquaria. One aquarium contained a perch (*Perca fluviatilis*) at least twice the length of the pikeperch that was placed in the other aquarium, smaller perch for smaller pikeperch and larger perch for the larger pikeperch. This size difference is sufficient for the perch to be able to consume a pikeperch (Dörner and Wagner 2003). The two short ends of the test aquarium containing the pikeperch were covered with black plastic sheets, with the long ends facing the perch and the observers uncovered. Three sides of the aquarium containing the perch was covered, with the long side facing the pikeperch aquarium uncovered. The bottom of the tank was covered with gravel. In the left-hand-side corner of the pikeperch aquarium, a plastic plant offering a possible refuge occupied approximately one third of the aquarium.

The perch was allowed to acclimatize in the test aquarium for one hour before the tests started, the pikeperch for 10 min. After 10 min, the divider was carefully removed, not to startle the fish, allowing visual contact between pikeperch and perch. The behaviour (Table 1) of the pikeperch was registered every 15 sec during 10 min. For each of the three rearing groups of pikeperch, 20 trials were run with one naïve fish in each trial.

Statistical analyses

Since, according to Shapiro-Wilk's test, the data were non-normally distributed, we used a non-parametric statistics. Fisher's exact test was used to compare the number of fish from different rearing groups performing a certain behaviour and Wilcoxon rank sum test was used to compare continuous variables representing different rearing groups. Bonferroni adjustment was applied in all pair-wise tests with three groups (exploratory behaviour and anti-predator response), to account for multiple comparison effect. This was done by calculating a new, adjusted critical p value of 0.017 (0.05 divided by 3) which was subsequently used to verify whether or not the test outcomes are significant. To evaluate the behavioural diversity of the different groups the Shannon index (Krebs 1989) was used. If results were expressed as percentages, the data were arcsin-transformed to obtain standard error values (*see* Sokal and Rohlf 1995).

Table 1. Behaviour observed during anti-predator response trials.

Active behaviour	
Skitter	rapid movements with frequent changes of direction
Dash	a single rapid directional movement
Inspection	swims toward and studies the larger fish/predator
Move away	the pikeperch moves directionally (decidedly) away from the predator
Inactive behaviour	
Hide	motionless or low activity within the refuge, occasional movement to place refuge in line of sight between the pikeperch and predator
Freeze	lying motionless on bottom or freezing mid motion outside of the refuge
Low activity	slow movement outside of the refuge

Results

Exploratory behaviour

On average, 72% of the fish left the start box, and there was no difference among fish of different origin in the number of fish that left the box (Fisher's exact test). For the fish that did leave the box, there was no significant difference between the groups in time before they left the box (Wilcoxon rank sum test). After exiting the start box, a fish either remained in the habitat it had entered or shifted at least once to a different habitat. The frequency of habitat shifts differed among groups, with the Pond 1 fish being significantly more active (Fig. 1).

There was a significant difference in the time spent in vegetation after leaving the start box between pond and tank-reared fish, but not between the two pond-reared fish groups (Fig. 2); the pond-reared fish used vegetation more than the tank-reared fish. There was no significant difference in the time spent in the start box area among all three groups of fish (Fig. 2). Tank-reared fish spent more time in the open-water section than the pond-reared fish, but the difference was not significant (Fig. 2).

Feeding on live prey

Ten feeding groups (5 fish each) were used from Pond 2 and Tank in the test. In aquaria with pikeperch from Pond 2, the first mysid was caught significantly faster than in the aquaria with tank-reared fish (n = 10, mean ± SE; 50 ± 16 sec, and 965 ± 214 sec, respectively; Wilcoxon rank sum test: $W_{10,10} = 0$, $p < 0.001$). In the tank-reared groups, it also took significantly longer time before all fish started to feed on the mysids as compared with the fish from the pond (n = 10,

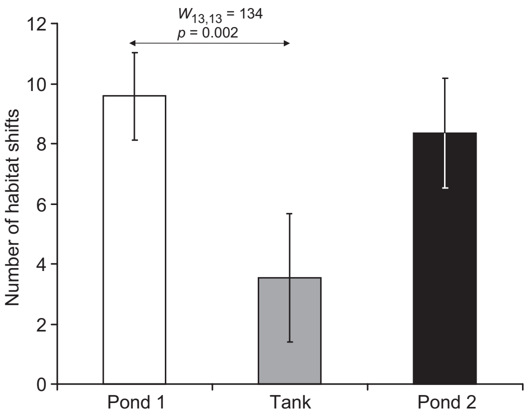

Fig. 1. Average number of habitat shifts performed by fish in the experimental aquaria. Results of the Wilcoxon rank sum test are shown in the figure (Bonferroni-adjusted critical $p = 0.017$).

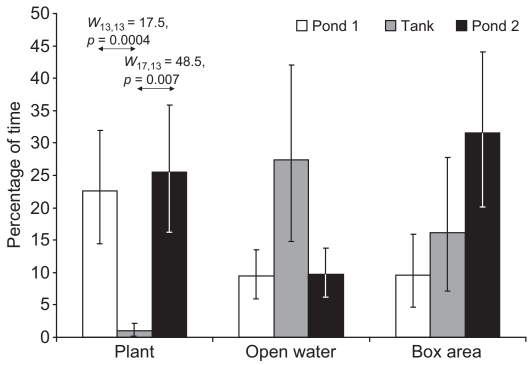

Fig. 2. Average fraction of time spent in vegetation, open water and box area for the three rearing groups of pikeperch during the exploration trials. Results of the Wilcoxon rank sum test are shown in the figure (Bonferroni-adjusted critical $p = 0.017$). Values were arcsine transformed according to Sokal and Rohlf (1995) to obtain standard error values.

mean ± SE; 2947 ± 239 sec, and 591 ± 192 sec, respectively; Wilcoxon rank sum test: $W_{10,10} = 0$, $p < 0.001$). In five out of the ten feeding groups of the tank-reared fish, at least one fish did not eat during the trial, but all pond-reared fish did eat (Fisher's exact test: $n_{\text{tank}} = n_{\text{pond2}} = 10$, $p = 0.033$). Fish that did not eat during the trial were considered as if they ate at the very end of the trial (i.e. they were assigned the value of 60 min). This assumption was used in the analysis of time until all fish in the trial started to feed.

Anti-predator response

Generally, the pond-reared fish were significantly more active in their response to the predator (Fig. 3), with most fish displaying at least some active behaviours (skitter, dash, inspection, move away, Table 1), whereas most of the tank-reared fish performed only passive behaviours (hide, freeze, low activity; Table 1 and Fig. 3).

When comparing the proportion of time spent performing behaviours separately, there was a significant difference between the pond- and the tank-reared fish in all behaviours but "freeze" and "hide" (Table 2 and Fig. 4). Pond 1 and 2 fish differed significantly in "low activity" and "freeze" behaviours (Table 2 and Fig. 4).

According to Shannon's diverity index, tank-reared fish displayed significantly more monotonous behaviour patterns than pond-reared fish

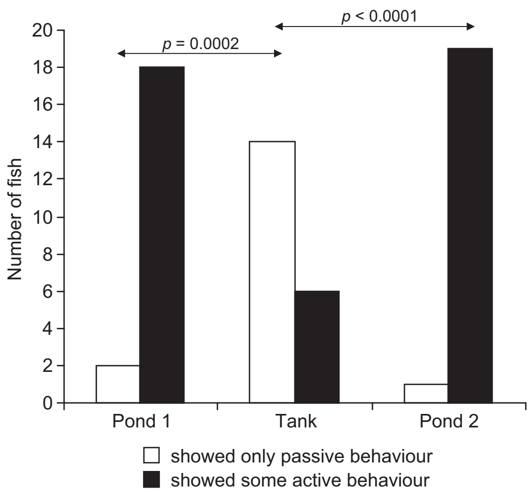

Fig. 3. Number of pikeperch from each rearing environment showing an active or passive response to the predator. Results of Fisher's exact test are shown in the figure (Bonferroni-adjusted critical $p = 0.017$); $n = 20$.

(*see* Table 3) and showed a strong tendency towards passive behaviour, especially "freeze", spending on average 61% of the time motionless outside the refuge (Fig. 4) and no skittering; there was also only one individual which performed a dash (Fig. 4). The most common anti-predator behaviour for pond-reared fish was "hide" but pond-reared fish had significantly more transitions between different behaviours (Fig. 5) and allocated their time more evenly between behaviours (*see* Table 3).

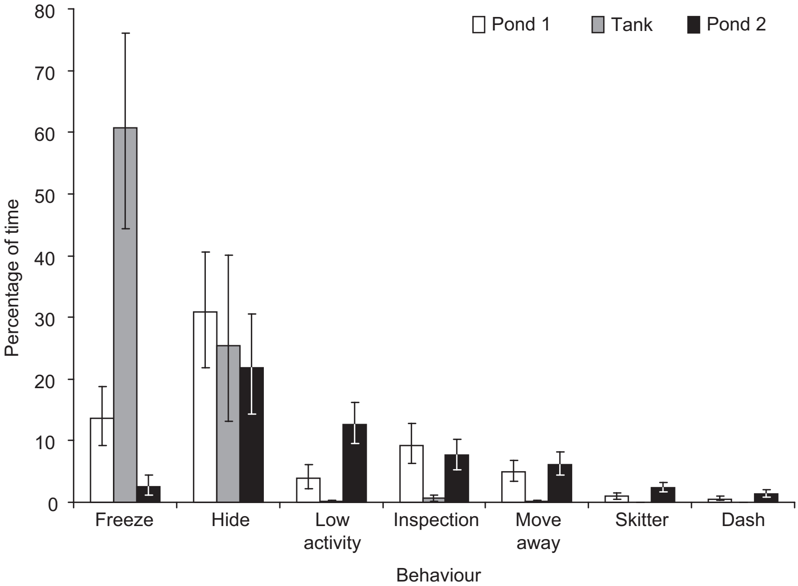

Fig. 4. Average fraction of time spent performing each behaviour by each rearing group of pikeperch during the predator-response trials. Values were arcsine-transformed to obtain standard error values. For significance of differences *see* Table 2.

Discussion

In our three experiments, clear behavioural differences between pond- and tank-reared fish were observed. The two pond-reared groups behaved similarly and significantly differently from the tank-reared group, indicating that the rearing environment affects the behaviour of the YOY pikeperch. In all trials, pond-reared fish were more active and flexible in their responses than tank-reared fish, indicating that a generally more passive behaviour has developed in the plain hatchery environment. The environmental complexity and variability is the most prominent difference between the rearing environments, ponds being closer to a natural environment, even including other fish species such as tench (*Tinca tinca*). There were also large differences in size between the tank and pond fish. The tank-reared fish grew larger than the pond-reared fish possibly because higher spatial and temporal variability in food distribution in the pond forced fish to spend more energy on foraging (Ryer and Olla 1996). It is also possible that fish in enriched environments spend more time on activities other than foraging. The larger size of the tank-reared fish is hence also a consequence of the rearing environment.

Exploratory behaviour

When introduced into a new environment it is

Table 2. Differences in average fraction of time spent displaying each behaviour by the three rearing groups of pikeperch during the predator-response trials evaluated by Wilcoxon rank sum test ($n = 20$). Bonferroni-adjusted critical $p = 0.017$.

	Pond 1 *vs.* Pond 2		Pond 1 *vs.* Tank		Pond 2 *vs.* Tank	
	W	*p*	*W*	*p*	*W*	*p*
Freeze	288	0.014	265	0.075	295.5	0.007
Hide	231	0.407	163.5	0.316	168	0.380
Low activity	107.5	0.011	108.5	0.005	51	< 0.001
Inspection	212	0.754	91	0.002	89.5	0.002
Move away	180	0.594	78	< 0.001	64	< 0.001
Skitter	250.5	0.155	110	< 0.001	60	< 0.001
Dash	170	0.382	110	< 0.001	102	0.001

important to get familiarised with the surroundings, to gain information about where to find food and refuge, and what potential risks are associated with the new area. Here an active but not overly risk-taking behaviour should be beneficial. In contrast to what was found in some earlier studies (e.g. Braithwaite and Salvanes 2005) where fish from enriched environments were faster to enter a new environment, in our exploratory-behaviour test the pond- and tank-reared fish did not differ in their willingness to leave the start box, which indicates no difference in explorative capacity between them. However, their behaviour after leaving the box was significantly different. The pond-reared fish were more active, moving around the aquaria between refuges, utilising both the plant and the area around the start box, whereas the tank-reared fish did not explore the environment to the same extent. Archard and Braithwaite (2011) showed that fish subjected to higher predation risks were more active and explorative. As there is a trade-off between risk of predation and loss of fitness due to reduced opportunities for e.g. foraging and mating when fishes are hiding from predators, fish from high-predation environments may be more active when they are not directly under threat. The observed cannibalism in the ponds may, therefore, have made the pond-reared fish more active. The rearing densities may also have affected the behaviour of the fish as the pond fish were reared at densities comparable to natural population densities whereas tank fish were reared at densities far from natural. Brockmark *et al*. (2010) investigated how rearing densities affected behavioural development and found that fry reared at natural densities were faster to find prey in a maze, indicating that they were more explorative.

The pond-reared fish used the vegetation as a refuge more often, indicating that they recognized vegetation as a potential shelter whereas the tank-reared fish had previously never been exposed to vegetation and quite seldom sought refuge in it during trials. Fish exposed to spatial heterogeneity in early life have been shown to be bolder but also to seek refuge faster than fish from a uniform environment (Salvanes and Braithwaite 2005). The start box could also be used as a refuge. There was, however, no significant difference in the use of the box area between pond and tank-reared fish. This could

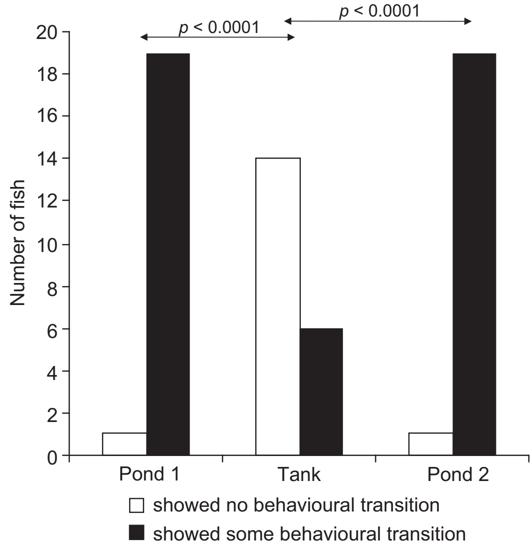

Fig. 5. Number of pikeperch from each rearing environment that performed at least one behavioural transition in response to the exposure to the predator. Results of Fisher's exact test are shown in the figure (Bonferroni-adjusted critical $p = 0.017$); $n = 20$.

Table 3. Shannon index of the behavioural divesity of the twenty fish from each breeder tested in the anti-preator tials. (Wilcoxon rank sum test: Pond 1 *vs*. Tank: $W_{20,20} = 38$, $p < 0.0001$; Pond 2 *vs*. Tank: $W_{20,20} = 366$, $p < 0.0001$; Pond 1 *vs*. Pond 2: $W_{20,20} = 206.5$, $p = 0.871$). Bonferroni-adjusted critical $p = 0.017$.

Fish no.	Pond 1	Tank	Pond 2
1	1.1	1.1	0.9
2	1.3	0	0
3	1.3	0	1.3
4	1.2	0.8	1.4
5	1.7	0	1.4
6	1.4	0	1.1
7	0.3	0.1	1.1
8	0	0	1.1
9	1.5	0	1.2
10	1.1	0	1.2
11	1.5	0	0.9
12	0.6	0	1.3
13	0.7	0	1.0
14	1.3	0	0.5
15	0.8	0.3	1.4
16	1.1	1.2	1.3
17	0.2	0	1.2
18	1.2	0.4	1.56
19	1.1	0	0.9
20	0.3	0	0.2

be caused by the passive behaviour of the tank-reared fish as several fish settled on the bottom close to the box after leaving it and remained there for the entire duration of the trial. Several tank-reared fish also settled on the bottom in the open-water section of the tank after leaving the box, to remain motionless for the rest of the trial. This suggests that the box may not be perceived as a refuge or used as one by the tank-reared fish, and the relatively high amount of time spent in the refuge area is merely a result of where the fish happened to settle.

The pond fish spent less time in the open-water section of the test aquarium than the tank fish. As Salvanes and Braithwaite (2005) showed, cod reared in an enriched environment spent more time in shelter than cod reared in a plain hatchery environment. Utne-Palm (2001) further showed that prey fish tend to avoid habitats where they have encountered predators before, possibly explaining why the pond-reared fish seem to have avoided open water more than tank-reared fish. As pikeperch are pelagic predators that are sometimes cannibalistic (e.g. Dörner *et al.* 1999), it is not unlikely that the pond populations had been subjected to predation by conspecifics, whereas the tank-reared fish were fed to constant satiation to avoid cannibalism and suspected cannibals were removed at an early stage. The relatively high use of the open-water section by the tank-reared fish could also be a passive choice as described above. It could also indicate a more risk-taking behaviour. Larger fish are usually subjected to lower predation risks (e.g. Sogard 1997, Fairchild and Howell 2000) which might affect their latency to seek cover. Johnsson (1993) however found no significant difference in predation susceptibility between large and small juvenile rainbow trout (*Oncorhynchus mykiss*).

The relationship between body size and exploratory behaviour is not clear. Earlier studies are inconsistent on the effect of body size on boldness (e.g. Johanson 1993, Reinhardt and Healy 1998, Brown and Braithwaite 2004, Brown *et al.* 2007, Harris *et al.* 2010, Archard and Braithwaite 2011). Brown and Braithwaite (2004) found that smaller fish emerged from shelter sooner than larger fish possibly driven by a higher metabolic rate. Johnsson (1993) on the other hand found that larger rainbow trout juveniles were more risk taking than small juveniles in order to get access to food in the presence of a predator.

Feeding on live prey

As shown by Braithwaite and Salvanes (2005), early environmental variability has positive effects on attraction to and consumption of live prey. This is in accordance with our findings as the pikeperch reared in a semi-natural pond environment started to feed on mysids, a novel food source, significantly faster than the tank-reared fish. The tank-reared fish were also observed to be slower in showing interest in the mysids as evidenced by approaching or tracking. The pond-reared fish have experienced an environment with variable spatial and temporal food supply as well as variation in food items, which appears to have made the fish more motivated to investigate potential new food items. Brown *et al.* (2003b) showed that only fish with both variable environment and variable food were able to generalize from one live prey to another despite previous live-prey experience. For hatchery-reared fish, that have been fed non-living food, it can be a challenge to start catching live prey although studies have shown that such fish can adapt to this quite quickly (Paszkowski and Olla 1985) indicating that the innate attraction to live prey persists also in hatchery stocks. However, there are also studies showing that not all fish from a hatchery succeed in the transition to live prey. In hatchery reared tiger muskellunge (*Esox masquinongy* × *E. lucius*), 11% of the tested individuals had not switched from pellet to live food after 14 days (Gillen *et al.* 1981) indicating that all individuals may not adapt to natural diet after stocking. A slower transition rate is also indicated in our results, where in 50% of the tank-reared test groups at least one individual had not caught a prey during the 1-h trial period, while all the pond-reared fish had caught prey well before the trial period ended.

The fish from the two breeders tested in this experiment were of different size and condition, which might have affected their motivation to feed on mysids as smaller fish have a higher metabolic rate (e.g. Clarke and Johnston 1999). However, it might not be the only explanation to the large behavioural difference regarding a novel prey as seen in our study. Hunger and stomach fullness are factors influencing motivation to eat (e.g. Colgan 1993). All the fish in our experiment had been starved for 24 hours to increase feeding motivation. Thus, we assume that the tank and pond fish were similarly motivated to feed during the trials. The larger tank fish should have higher foraging rates than the pond ones, as larger fish e.g. have larger gape size and shorter handling time (Scharf *et al.* 1998, Vucic-Pestic *et al.* 2010), but this was not seen in our trials. In a study by Braithwaite and Salvanes (2005), there were also significant differences in fish size between rearing environments, hatchery fish being larger than fish from enriched environments; here only the fish from the most enriched environment with variable food and spatial clues, corresponding closely to the pond-reared fish, were significantly faster at responding to live prey. Rearing density could also have influenced the attraction to live prey. Brockmark *et al.* (2010) showed that trout parr reared at natural density were faster to eat novel prey than parr reared at hatchery densities.

Anti-predator response

Successful predator defence depends on the prey's ability to assess and respond to changes in predation risk. Fish use olfaction, vision and tactile senses to assess their environment and detect predators (Pitcher 1986). Even though a combination of cues reveals more about the predator (Martin *et al.* 2010), the majority of prey fishes have excellent vision (Guthrie 1993), allowing them to respond to visual cues alone. Prey fish seem to be predisposed to respond to visual cues based on some generalized predator features such as body shape and colour, and shape and size of the mouth (Karplus *et al.* 1982, Magurran and Girling 1986). Responding to general facial cues reduces the need for recognizing species-specific cues. In our study, the pond-reared fish were more prone to perform active behaviour, including predator inspection. Visual cues often elicit predator-inspection behaviour, i.e. approaching and swimming slowly along the predator before returning to the shoal (Pitcher *et al.* 1986). This might signal to the predator that it had been detected as well as allowing the prey fish to assess the predator's condition and motivation to attack. Prey fish discriminate between hungry and satiated predators and seem able to assess the predator's level of attack motivation by its behaviour, inducing a stronger anti-predator response toward hungry predators than satiated ones (Helfman 1989, Licht 1989). The higher proportion of predator inspection in the pond-reared fish may give them a better perception of the risk imposed by an individual approaching.

The tank-reared fish had a generally less active anti-predator response, keeping a low profile, predominately remaining motionless. This is in accordance with earlier results reported by Salvanes and Braithwaite (2005) where fish from enriched environments had a stronger anti-predator response than fish from plain environments.

Despite the pond-reared fish being more active when exposed to a predator, there were certain behaviours that did not differ significantly between the groups, e.g. there was no significant difference between pond-reared and tank-reared fish in the behaviour "hide" (staying in plant refuge). Contrary to our results, Krause *et al.* (1998) and Lundvall *et al.* (1999) observed that large fish spent more time in shelter than small fish when exposed to a predator. Krause *et al.* (1998) suggested that large fish were less affected by food deprivation allowing a more passive anti-predator behaviour. On the other hand, Salvanes and Braithwaite (2005) did not find any significant differences in recovery from being chased by a simulated predator between cod (*Gadus morhua*) from a homogeneous and a heterogeneous rearing environments despite the size difference between the groups. Fish from the heterogeneous environment did however use shelter more. They also found that size did not affect basic activities of the fish, their use of shelter or their recovery after stress. Laakkonen and Hirvonen (2007) compared boldness to predator cues of the fast- and slow-growing individuals of Arctic char (*Salvelinus alpinus*) reared in captivity, but found no correlation between boldness and growth rate. These findings are interesting in relation to our results as the size difference between the pond and tank fish can be argued to have an effect on the behaviour. The lack of difference in shelter use in our study is probably caused by the passive behaviour of the tank group that often just settled on the bottom when released in the middle of the test aquarium, sometimes landing in the vegetation, being registered as "hide", sometimes landing outside the vegetation, being registered as "freeze".

"Freeze" was the other behaviour that was not significantly different between Pond 1 fish and Tank. Pond 1 fish did however display a somewhat different pattern of "freeze". Tank fish often performed "freeze" during the whole trial lying on the bottom, whereas pond fish never froze for a whole trial but rather performed shorter periods of "freezing", often lasting for just a few seconds and more often "freezing" in the water column. Several of the tank-reared fish did not display any other behaviour than "freeze", not even moving away when the predator approached and showed a clear interest. To be motionless could be an effective strategy to avoid predators, e.g. predators that are sensitive to prey movement. On the other hand remaining stationary for longer periods might result in odour accumulation, attracting predators sensitive to smell. The more monotonous response from tank-reared fish is also evident from the low frequency of behavioural transitions. Pond-reared fish had a higher frequency of behavioural transitions and displayed all measured behaviours, indicating a higher behavioural flexibility than tank-reared fish. Salvanes *et al.* (2007) also found that plain-reared fish have a more rigid response to predators as the shoaling tendency of fish reared in enriched tanks varied between testing environments, whereas fish reared in plain environments responded in the same way irrespective of the testing environment. Although we did not test the anti-predator behaviour of our fish in more than one environment, they seem to be less behaviourally flexible than pond fish, a trend which prevailed through all of our behavioural trials.

It is acknowledged that anti-predator responses are weaker in hatchery-reared than in wild fish (e.g. Howell 1994). In our study, the pond fish have been reared in semi-natural environments and can hence be comparable to wild fish. In a study by Malavasi *et al.* (2004) where wild and hatchery fish of the same size were compared, the wild fish had a stronger anti-predator response, which indicates that the environment rather than the size is responsible for the diference in reaction to preadators, which is in accordance with our hypothesis of rearing environments affecting behaviour. It could be argued that different environmental conditions facilitate different anti-predator behaviours and that the tank fish did not have a weaker response but rather adjusted to their environment. Templeton and Shriner (2004) compared the anti-predator response of two populations of guppies and found that "freeze" response was most common towards avian predators and predator inspection was the most common response towards fish predator. As the tank fish were not subjected to any kind of predator this could not directly explain their high amount of "freeze".

Although not quantified, the pikeperch behaviour was observed during acclimatization in the anti-predator test. During this period, the fish behaved much as they had in the exploration test. The pond fish moved around the aquaria, appearing to investigate their new environment, whereas tank fish more often lay motionless on the bottom. The fish that lay on the bottom before exposure to predator very often continued to do so during exposure. It is hence not clear whether the behaviour indicates that tank pikeperch do not perceive the perch as a threat or was "freezing" a response to the predator. It can be argued that the fish did not feel threatened due to the fact that larger fish usually are subjected to lower predation risk (e.g. Kruase *et al.* 1998), but as the size difference between perch and pikeperch was proportionally equal in all groups this should not be a problem. There were also occasions when the perch tried to attack the tank-reared pikeperch through the glass and still the pikeperch did not move, indicating that the pikeperch did not perceive the perch as a threat. This degree of passiveness seems perilous and would impose high risk of mortality if maintained in the wild. Brown *et al.* (2006) showed that the minimum level of predator stimulus triggering anti-predator response was lower in fish from high background predation risk than low background predation risk. The fact that there were significant differences in size between all the groups, and that the two pond-reared fish groups behaved similarly, indicates that rearing environment rather than size was affecting anti-predator responses of the fish.

Naïve fish can modify their behaviour through social learning, observing experienced fish react fearfully towards a stimulus. This is an important way in which fish can learn anti-predator responses, and several studies have documented this process (Krause 1993, Chivers and Smith 1995, Mathis *et al*. 1996, Kelly *et al*. 2003). This type of learning has probably been acting in the pond groups where cannibalism from larger con-specifics occurred to some extent. It is reasonable to think that predation from larger con-specifics in the ponds could have improved vigilance and anti-predator responses even to hetero-specifics, as the present results are indicating. As discussed above, fish from high-predation populations were found to be bolder, more explorative and more active than those from low-predation populations, independent of body size (Archard and Braithwaite 2011). Miklósi *et al*. (1997) revealed that the continuous exposure to con-specific larvae was the main cause among paradise fish (*Macropodus opercularis*) for the reduced anti-predator behaviour toward a predator model. This could also have influenced the behavioural differences seen between pond and tank fish as they had experienced very different rearing densities. Brockmark *et al*. (2010) also describe a more efficient anti-predator behaviour in fish reared in natural densities.

Implications for stocking

A fast transition to a new diet is beneficial when being moved to a new area by stocking. Several studies have shown that shortly after release hatchery fish show lower consumption (e.g. Bachman 1984), fewer prey types consumed (e.g. Sosiak *et al*. 1979), slower transition to a new prey type and lower growth rate and survival (e.g. Ersback and Haase 1983) than wild fish. Reared cod have been proved to eat slower moving prey shortly after release than wild fish do, however the difference disappeared after a month (Nordeide and Salvanes 1991). Hatchery reared salmonids were shown to position themselves differently than wild fish in the habitat when released, affecting foraging, metabolic demands and predator vulnerability (Sosiak *et al*. 1979, Bachman 1984, Maynard *et al*. 1996b). This may also indicate a lower explorative motivation in the hatchery-reared fish making them utilize the habitat sub-optimally, which is also indicated by our results.

Predation is one of the major causes of mortality of hatchery fish, that occurring shortly after release (e.g. Fisher and Pearcy 1988). To have a well developed anti-predator behaviour is the most important life skill in stocked fish as starvation is not an immediate threat to survival but predation is. Although the tank-reared fish have never experienced predation or live prey in their rearing environment, after release they will have an opportunity to observe more experienced fish and learn to react correctly to predators and prey. Even so, they will be lagging behind in experience as compared with the pond-reared fish.

The use of hatchery fish in supplementing wild populations is debated regarding survival of the stocked fish as well as genetic and behavioural effects imposed by the survivors (e.g. Kellison *et al*. 2000, Huntingford 2004, Dannewitz *et al*. 2010). Our results suggest that fish from a plain hatchery environment were less suitable for stocking as they display a very uniform and passive behaviour in all tests when compared with that of the pond-reared fish. Fish used for stocking need to be flexible and be able to learn to cope in their new environment. Increasing levels of complexity and variability in the rearing environment can increase the capacity to learn in fish (Spence *et al*. 2011). Early experience of environmental variability in cod has been proved to affect consumption of live prey, speed of exploration of a new environment, recovery from simulated predator attack (Braithwaite and Salvanes 2005), as well as social learning (Salvanes and Braithwaite 2005). Even though learning is costly, fish that are able to learn and adapt their behaviour are more likely to survive in the wild.

Both field and laboratory studies on juvenile fishes generally support the idea of “bigger is better", as larger members of a cohort can better tolerate physical extremes and endure longer periods without food as compared with smaller conspecifics (Sogard 1997). Increased growth may however affect behavioural development and the advantages of large size may be outweighed by the advantages of more refined antipredator behaviours.

This study shows clear behavioural differences between pond reared and tank-reared fish. As several factors differ between these rearing environments e.g. environmental complexity, rearing densities, growth rate and predation, it is impossible to distinguish one process that is responsible for the behavioural differences seen between the groups. It is more likely that they are all contributing. However, if we aim at applying the results in the rearing and stocking practises, it is of less importance if the behavioural differences are due to one or several of these factors as pond and tank-reared fish are, at the stocking occasion, behaving differently. The results also challenge the present tendency of replacing the traditional rearing of pikeperch in semi-natural outdoor ponds with more intensive indoor hatchery production, where the fish may lose the opportunity to learn to use natural food, find shelter and avoid predators, ultimately increasing the mortality risk of these fish when stocked.

Acknowledgement: We would like to thank the breeders for providing fish for the experiments. We are grateful to Aquaria Vattenmuséum for providing material, housing and excellent service during the experiment and to Bertil Borg for providing test aquaria. We would also like to thank the editor Dr. Outi Heikinheimo, the reviewers and prof. Sture Hansson for invaluable comments on the manuscript. This project was funded by Baltic Sea 2020 as part of the project 'Pikeperch in Himmerfjärden'.

References

Archard G.A. & Braithwaite V.A. 2011. Increased exposure to predators increases both exploration and activity level in *Brachyrhaphis episcope*. *J. Fish Biol.* 78: 593–601.

Bachman R.A. 1984. Foraging of free-ranging wild and hatchery brown trout in a stream. *Trans. Am. Fish. Soc.* 113: 1–32.

Berejikian B.A. 1996. Instream postrelease growth and survival of chinook salmon smolts subjected to predator training and alternate feeding strategies. In: Maynard D.J., Flagg T.A. & Mahnken C.V. (eds.), *Development of a natural rearing system to improve supplemental fish quality, 1991–1995*, Report to Bonneville Power Administration, Contract DE-A179-91BP20651, pp. 113–127.

Braithwaite V.A. & Salvanes A.G.V. 2005. Environmental variability in early rearing environment generates behaviourally flexible cod: implications for rehabilitating wild populations. *Proc. R. Soc. B* 272: 1107–1113.

Braithwaite V.A. & Salvanes A.G.V. 2008. Cognition: learning and memory. In: Magnhagen C., Braithwaite V.A., Forsgren E. & Kapoor B.G. (eds.), *Fish behaviour*, Science Publishers, Enfirld NH, pp. 33–60.

Brockmark S., Adriaenssens B. & Johnsson J.I. 2010. Less is more: density influences the development of behavioural life skills in trout. *Proc. R. Soc. B* 277: 3035–3043.

Brown C. & Braithwaite V.A. 2004. Size matters: a test of boldness in eight populations of the poeciliid *Brachyraphis episcope*. *Anim. Behav.* 68: 325–1329.

Brown C., Burgess F. & Braithwaite V.A. 2007. Heritable and experiential effects on boldness in a tropical poeciliid. *Behav. Ecol. Sociobiol.* 62: 237–243.

Brown C., Davidson T. & Laland K. 2003b. Environmental enrichment and prior experience of live prey improve foraging behaviour in hatchery-reared Atlantic salmon. *J. Fish Biol.* 63: 187–196.

Brown C., Markula A. & Laland K. 2003a. Social learning of prey location in hatchery-reared Atlantic salmon. *J. Fish Biol.* 63: 738–745.

Brown G.E., Rive A.C., Ferrari M.C.O. & Chivers D.P. 2006. The dynamic nature of antipredator behavior: prey fish integrate threat-sensitive antipredator responses within background levels of predation risk. *Behav. Ecol. Sociobiol.* 61: 9–16.

Brännäs E. & Johnsson J.I. 2008. Behaviour and welfare in farmed fish. In: Magnhagen C., Braithwaite V.A., Forsgren E. & Kapoor B.G. (eds.), *Fish behaviour*, Science Publishers, Enfirld NH, pp. 593–627.

Chivers D.P. & Smith J.F. 1995. Chemical recognition of risky habitats is culturally transmitted among fathead minnows, *Pimephales promelas* (Osteichthyes, Cyprinidae). *Ethology* 99: 286–296.

Clarke A. & Johnston N.M. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. *J. Anim. Ecol.* 68: 893–905.

Colgan P. 1993. The motivational basis of fish behaviour. In: Pitcher T.J. (ed.), *Behaviour of teleost fishes*, Chapman & Hall, London, pp. 31–55.

Coolen I., van Bergen Y., Day R.L. & Laland K.N. 2003. Species difference in adaptive use of public information in sticklebacks. *Proc. R. Soc. Lond. B* 270: 2413–2419.

Dannewitz J., Prestegaard T. & Palm S. 2010. *Långsiktigt hållbar gösförvaltning. Genetiska data ger ny information om bestånd och effekter av utsättning*. Fiskeriverket Rapport Finfo 2010:3.

Dörner H. & Wagner H. 2003. Size-dependent predator–prey relationships between perch and their fish prey. *J. Fish Biol.* 62: 1021–1032.

Dörner H., Wagner A. & Benndorf J. 1999. Predation by piscivorous fish on age-0 fish: spatial and temporal variability in a biomanipulated lake (Bautzen reservoir, Germany). *Hydrobiol*. 408/409: 39–46.

Einum S. & Fleming A. 1997. Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. *J. Fish Biol*. 50: 634–651.

Ellis, T. & Gibson R.N. 1995. Size-selective predation of O-group flatfishes on a Scottish nursery ground. *Mar. Ecol. Prog. Ser*. 127: 27–37.

Ersback K. & Haase B.L. 1983. Nutrient deprivation after stocking as a possible mechanism leading to mortality in stream-stocked brook trout. *N. Am. J. Fish. Manage*. 3: 142–151.

Fairchild E.A. & Howell W.H. 2000. Predator–prey size relationship between *Pseudopleuronectes americanus* and *Carcinus maenas*. *J. Sea Res*. 44: 81–90.

Fisher J.P. & Pearcy W.G. 1988. Growth of juvenile coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington, USA, in years of different coastal upwelling. *Can. J. Fish. Aquat. Sci*. 45: 1036–1044.

Gillen A.L., Stein R.A. & Carline R.F. 1981. Predation by pellet-reared tiger muskellunge on minnows and bluegills in experimental systems. *Trans. Am. Fish. Soc*. 110: 197–209.

Guthrie D.M. 1993. Role of vision in fish behaviour. In: Pitcher T.J. (ed.), *The behaviour of teleost fishes*, Chapman & Hall, London, pp. 89–127.

Harris S., Ramnarine I.W., Smith H.G. & Pettersson L.B. 2010. Picking personalities apart: estimating the infl uence of predation, sex and body size on boldness in the guppy *Poecilia reticulate*. *Oikos* 119: 1711–1718.

Helfman G.S. 1989. Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. *Behav. Ecol. Sociobiol*. 24: 47–58.

Howell B.R. 1994. Fitness of hatchery-reared fish for survival in the sea. *Aquacult. Fish. Manage*. 25: 3–17.

Huntingford F.A. 2004. Implications of domestication and rearing conditions for the behaviour of cultivated fishes. *J. Fish Biol*. 65: 122–142.

Johnsson I.J. 1993. Big and brave: size selection affects foraging under risk of predation in juvenile rainbow trout, *Oncorhynchus mykiss*. *Anim. Behav*. 45: 1219–1225.

Juanes F. & Conover D.O. 1994. Piscivory and prey size selection in young-of-the-year bluefish: predator preference or size-dependent capture success? *Mar. Ecol. Prog. Ser.* 114: 59–69.

Karplus I., Goren M. & Algom D. 1982. A preliminary experiment analysis of predator face recognition by *Chromis caerulus* (Pisces, Pomacentridae). *Z. Tierpsychol*. 58: 53–65.

Kellison G.T., Eggleston D.B. & Burke J.S. 2000. Comparative behaviour and survival of hatchery-reared versus wild summer flounder (*Paralichthys dentatus*). *Can. J. Fish. Aquat. Sci*. 57: 1870–1877.

Kelly J.L., Evans L.P., Ramnarine I.W. & Magurran A.E. 2003. Back to school: can antipredator behaviour in guppies be enhanced through social learning? *Anim. Behav*. 65: 655–662.

Kelly J.L., Magurran A.E. & Macías-Garcia C. 2005. The influence of rearing experience on the behaviour of an endangered Mexican fish, *Skiffia multipunctata*. *Biol. Conserv*. 122: 223–230.

Kishlinger R.L. & Newitt G.A. 2006. Early rearing environment impacts cerebellar growth in juvenile salmon. *J. Exp. Biol*. 209: 504–509.

Krause J. 1993. Transmission of fright reaction between different species of fish. *Behaviour* 127: 37–48.

Krause J., Loader S.P., McDermott J. & Ruxton G.R. 1998. Refuge use by fish as a function of body length-related metabolic expenditure and predation risks. *Proc. R. Soc. Lond. B* 265: 2373–2379.

Krebs C.J. 1989. *Ecological methodology*. — Harper and Row Publishers, New York.

Kreuger C.C. & May B. 1991 Ecological and genetic effects of Salmonid introduction in North America. *Can. J. Fish. Aquat. Sci*. 48 (Suppl. 1): 66–77.

Laakkonen M.V.M. & Hirvonen H. 2007. Is boldness towards predators related to growth rate in naïve captive-reared Arctic char (*Salvelinus alpinus*)? *Can. J. Fish. Aquat. Sci*. 64: 665–671.

Licht T. 1989. Discrimination between hungry and satiated predators: the response of guppies (*Poecilia reticulata*) from high and low predation sites. *Ethology* 82: 238–243.

Lundvall D., Svanbäck R., Persson L. & Byström P. 1999. Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. *Can. J. Fish. Aquat. Sci*. 56: 1285–1292.

Magnhagen C., Braithwaite V.A., Forsgren E. & Kapoor B.G. 2008. *Fish behaviour*. Science Publishers, Enfirld, NH.

Magurran A.E. & Girling S.L. 1986. Predator model recognition and response habituation in shoaling minnows. *Anim. Behav.* 34: 510–518.

Malavasi S., Georgalas V., Lugli M., Torricelli P. & Mainardi D. 2004. Differences in the pattern of antipredator behaviour between hatchery-reared and wild European sea bass juveniles. *J. Fish Biol*. 65 (Supplement A): 143–155.

Martin C.W., Fodrie F.J., Heck K.L. & Mattila J. 2010. Different habitat use and antipredator response of juvenile roach (*Rutilus rutilus*) to olfactory and visual cues from multiple predators. *Oecologia* 162: 893–902.

Mathis A., Chivers D.P. & Smith J.F. 1996. Cultural transmission of predator recognition in fishes: intraspecific and interspecific learning. *Anim. Behav.* 51: 185–201.

Maynard D.J., Tezak E.P., Berejikian B.A. & Flagg T.A. 1996a. The effect of feeding spring Chinook salmon a live-food supplemented diet during acclimation, 1995. In: Maynard D.J., Flagg T.A. & Mahnken C.V. (eds.), *Development of a natural rearing system to improve supplemental fish quality, 1991–1995*, Report to Bonneville Power Administration, Contract DE-A179-91BP20651, pp. 98–112.

Maynard D.J., Crewson M., Tezak E.P., McAuley W.C., Schroder S.L., Knudsen C., Flagg T.A. & Mahnken C.V. 1996b. The postrelease survival of Satsop river fall Chinook salmon reared in conventional and seminatural raceway habitats, 1994. In: Maynard D.J., Flagg T.A. & Mahnken C.V. (eds.), *Development of a natural rearing system to improve supplemental fish quality, 1991–1995*, Report to Bonneville Power Administration, Contract DE-A179-91BP20651, pp. 78–97.

McGurk M.D. 1986. Natural mortality of marine pelagic fish eggs and larvae, role of spatial patchiness. *Mar. Ecol. Prog. Ser.* 34: 227–242.

Miklósi Á., Pongrácz P. & Csányi V. 1997. The ontogeny of antipredator behavior in paradise fish larvae (*Macropodus opercularis*) IV. The effect of exposure to siblings. *Develop. Psychobiol.* 30: 283–291.

Nordeide J.T. & Salvanes A.G.V. 1991. Observations on reared newly released and wild cod (*Gadus morhua* L.) and their potential predators. *ICES Mar. Sci. Symp.* 192: 139–146.

Paszkowski C.A. & Olla B.L. 1985. Foraging behavior of hatchery-produced coho salmon (*Oncorhynchus kisutch*) smolt on live prey. *Can. J. Fish. Aquat. Sci.* 42: 1915–1921.

Pitcher T.J. 1986. *The behaviour of teleost fishes*. Croom Helm, London.

Pitcher T.J., Green D.A. & Magurran A.E. 1986. Dicing with death: predator inspection behaviour in minnow shoals. *J. Fish Biol.* 28: 439–448.

Reinhardt U.G. & Healy M.C. 1999. Season- and size-dependent risk taking in juvenile coho salmon: experimental evaluation of asset protection. *Anim. Behav.* 57: 923–933.

Ryer C.H. & Olla B.L. 1996. Growth depensation and aggression in laboratory reared coho salmon: the effect of food distribution and ration size. *J. Fish Biol.* 48: 686–694.

Salvanes A.G.V. & Braithwaite V.A. 2005. Exposure to variable spatial information in the early rearing environment generates asymmetries in social interactions in cod (*Gadus morhua*). *Behav. Ecol. Sociobiol.* 59: 250–257.

Salvanes A.G.V., Moberg O. & Braithwaite V.A. 2007. Effects of early experience on group behaviour in fish. *Anim. Behav.* 74: 805–811.

Scharf F.S., Buckel J.A., Juanes F. & Conover D.O. 1998. Predation by juvenile piscivorous bluefish (*Pomatomus saltatrix*): the influence of prey to predator size ratio and prey type on predator capture success and prey profitability. *Can. J. Fish. Aquat. Sci.* 55: 1695–1703.

Sogard S.M. 1997. Size-selective mortality in the juvenile stage of teleost fished: a review. *Bull. Mar. Sci.* 60: 1129–1157.

Sokal R.R. & Rohlf F.J. 1995. *Biometry: the principles and practices of statistics in biological research*, 3rd ed. W.H. Freeman and Company, New York.

Sosiak A.J., Randall R.G. & McKenzie J.A. 1979. Feeding by hatchery-reared and wild Atlantic salmon (*Salmo salar*) parr in streams. *J. Fish. Res. Bd. Can.* 36: 1408–1412.

Spence R., Magurran A.E. & Smith C. 2011. Spatial cognition in zebrafish: the role of strain and rearing environment. *Anim. Cogn.* 14: 607–612.

Strand D., Utne-Palm A.C., Jakobsen P.J., Braithwaite V.A., Jensen K.H. & Salvanes A.G.V. 2010. Foraging skills are affected by exposure to habitat complexity in Atlantic cod. *Mar. Ecol. Prog. Ser.* 412: 273–282.

Templeton C.N. & Shriner W.M. 2004. Multiple selection responses influence Trinidadian guppy (*Poecilia reticulate*) antipredator behaviour. *Behav. Ecol.* 15: 673–678.

Utne-Palm A.C. 2001. Response of naïve two-spotted gobies *Gobiusculus flavescens* to visual and chemical stimuli of their natural predator, cod *Gadus morhua*. *Mar. Ecol. Prog. Ser.* 218: 267–274.

Vilhunen S. 2006. Repeated antipredator conditioning: a pathway to habituation or to better avoidance? *J. Fish Biol.* 68: 25–43.

Vucic-Pestic O., Rall B.C., Kalinkat G. & Brose U. 2010. Allometric functional response model: body masses constrain interaction strengths. *J. Anim. Ecol.* 79: 249–256.